

FLOWERING MORPHOLOGY, PHENOLOGY AND FLOWER VISITORS OF THE AUSTRALIAN RAINFOREST TREE *RYPAROSA KURRANGII* (ACHARIACEAE)

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Abstract

The understorey tree *Ryparosa kurrangii* B.L. Webber (Achariaceae) is restricted to a limited number of populations in three distinct valleys of lowland tropical rainforest in northern Queensland, Australia. To provide baseline information for determining potential pollen vectors and the opportunity for inter-population gene flow, flowering morphology, phenology and flower visitation were studied in natural populations over a number of seasons. Contrary to all previous work, *R. kurrangii* was found to be monoecious, with temporally separated flushes of staminate and carpellate flowers. Flower production was primarily basicauliflorous on the main trunk with small open flowers borne on long racemes. Heavy nocturnal scented nectar production coincided with peak animal visitation. Predominant flower visitors were adults of an undescribed species of *Monolepta* Chevrolat *sensu lato* (Coleoptera: Chrysomelidae: Galerucinae) and nymphs of *Coridzolon australiense* Carvalho & Gross (Heteroptera: Miridae: Mirinae: Hyalopeplini). Now that the floral biology and morphology as well as the dominant flower visitors of *R. kurrangii* have been documented, further work is required to determine the likely contribution of flower visitors to pollination events and population gene flow.

Introduction

The wet tropical rainforests of northern Queensland comprise just 0.1% of the land surface yet contain 25% of all plant genera found in Australia (Keto and Scott 1986). In tropical rainforests, plant-pollinator and plant-frugivore interactions are vital for ensuring genetic variation in plant populations through outcrossing (*e.g.* Janzen 1983, Bodmer 1991, Mack 1993, Corlett 2001, Brewer and Webb 2002, Peres and van Roosmalen 2002).

Ryparosa kurrangii B.L. Webber (Achariaceae; Flacourtiaceae *pro parte*) is a rare sub-canopy tree restricted to tropical lowland rainforest of the Daintree region. The taxon is likely to depend closely on the endangered cassowary (*Casuaris casuaris johnsonii*; a large flightless bird) for long distance seed dispersal (Webber and Woodrow 2004). However, continued development in the Daintree lowlands is encroaching on current *R. kurrangii* populations and the resulting disturbance appears to be having a detrimental effect on what might be a significant interaction for *R. kurrangii* with the increasingly endangered cassowary (B.L. Webber, pers. obs.). Therefore, any inter-population gene flow that results from pollination events will become increasingly important for maintaining genetic diversity, if the disruption of plant-frugivore interactions continues.

Previous taxonomic literature has highlighted how little is known about the life history of flowering in flacourtiaceous genera (van Slooten 1925, Sleumer 1954). Conflicting statements over monoecy or dioecy within species (e.g. Woodson and Schery 1968) may be attributed to the predominance of species descriptions relying largely on herbarium specimens over field-based observations. Even less is known about pollination vectors in the family. Thus, the aims of this current study were (1), to provide a detailed documentation of flowering morphology and phenology in *Ryparosa kurrangii* and (2), to determine flower visitors that might act as pollination vectors and provide opportunity for gene flow during flower fertilisation.

Methods

Field observations on the life history and developmental biology of *Ryparosa kurrangii* were made over six years (1998 to 2004), in the Daintree World Heritage area of northern Queensland, Australia (16°08'S, 145°26'E). The species is currently classified as rare by the Queensland Nature Conservation Act (Queensland Government 1992), although a higher conservation status might be required in light of recent work (Webber and Woodrow 2004, 2006, Webber 2005). *Ryparosa kurrangii* has a very restricted distribution and is only known from three distinct valleys comprising a small strip of coastal lowland tropical rainforest between the Daintree River and Cape Tribulation. Within these valleys, *R. kurrangii* is spatially rare but locally common, often forming discrete populations near creeks and ephemeral streams. Rainforest vegetation communities at all sites used in the study can be classed as complex mesophyll vine forest (CMVF, Type 1a) or mesophyll vine forest (MVF, Type 2a; *sensu* Tracey 1982).

Observations on reproductive biology, life history patterns and plant-animal interactions were made on eight tagged *R. kurrangii* populations across the three valleys, each comprising between 30 and 350 individuals. This allowed for the long-term monitoring of numerous individual trees (Webber 2005). More remote untagged populations were periodically examined within the wider Daintree lowlands region. Flowering phenology and morphology were documented on an *ad hoc* basis throughout flowering periods that occurred during the 6 years of study. Phenological variation in flowering patterns (the timing of distinct stages of floral development and flower anthesis within and between populations) was recorded at random intervals spaced throughout the flowering season. Nectar production was monitored during day visits to populations and also on night visits while observing flower visitation. Floral morphological data were collected from fresh flower racemes in the field and laboratory.

Flower visitation observations for male and female racemes were made both at night (between dusk to 00:30 and 04:00 to dawn) and during daylight hours. Visitation was recorded by observing individual trees for periods of at least 10 minutes, supplemented by random spot sweeps for the presence of

flower visitors on an individual tree at any one time. These observations were quantified, where possible, based on the number of individuals, their interactions with flower racemes (position on flowers, any characteristic behaviour or foraging activity) and subsequent movements between individual trees. Invertebrates collected from *R. kurrangii* flower racemes were identified from field-collected specimens either preserved in 70% ethanol or dry killed and mounted.

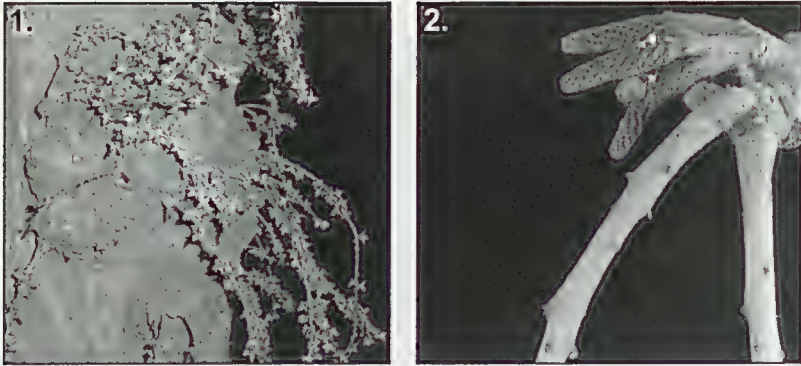
Voucher specimens for collected invertebrates were lodged at the Australian Museum, Sydney and the Australian National Insect Collection (ANIC), Canberra.

Results

Flower morphology and phenology

All eight permanently tagged populations of *R. kurrangii* were comprised of trees that were consistently monoecious. On individual trees, staminate and carpellate flower racemes were produced in distinctly separate temporal periods on all individuals observed. Staminate flowers appeared first and were temporally separated from mature carpellate flowers (which appeared as buds while staminate flowers were open) on the same individual by 3-4 weeks. Occasionally, individual trees produced two flushes of staminate flowers before a carpellate flush (within the same season), while other individual trees consistently produced heavier flushes of either staminate or carpellate flowers over a number of flowering seasons. Within populations and between populations in close proximity to each other (*i.e.* in the same valley) there was temporal overlap between staminate and carpellate racemes on different individual trees. However, flowering synchrony between populations in different valleys, although still temporally overlapping, was not as tightly synchronised.

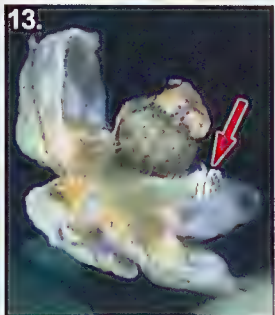
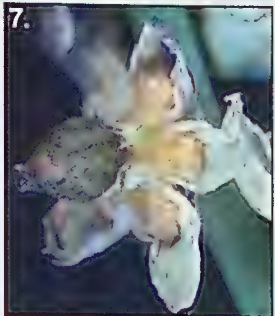
Flowering position was, for the most part, on the lower portion (2-3 m and sometimes up to 5 m) of the main trunk from distinctive tubercles (Fig. 1). On large individuals, these tubercles exceeded 150 x 150 mm and racemes were produced in fascicles of up to 5 from multiple points on each tubercle (Fig. 2). While staminate flowers (and very rarely carpellate flowers) were occasionally observed on small tubercles situated on side branches, flowering on side branches generally only occurred on younger trees with poorly developed trunk tubercles. Mature fruits were almost always observed on the main trunk. Flowering or fruiting was very rarely observed on trees smaller than 5 m in height and with a diameter at breast height (DBH) of less than approximately 50-60 mm. Raceme peduncles underwent significant elongation shortly before the flowers opened and, after flower anthesis, racemes with staminate flowers were generally 300-400 mm long; those with carpellate flowers were slightly shorter. On rare occasions, staminate and carpellate flower racemes in excess of 600 mm long were observed.



Figs 1-2. Floral raceme position on *Ryparosa kurrangii*. (1) flower racemes are generally borne on large distinctive tubercles on the lower portion of the main trunk; (2) racemes form in fascicles of up to five.

Flowers generally flushed in a spectacular display covering the trunk during the dry season of June to September (Fig. 3). Staminate flower buds were globose (Fig. 4), while carpellate buds were pyriform (Fig. 5). The calyx on both staminate and carpellate flowers was observed to irregularly rupture during floral anthesis (Fig. 6), to reveal carpellate flowers with short fleshy staminodes (Figs 7, 8) and staminate flowers with united filaments (Fig. 9). All recently opened flowers were heavy with nectar at night (Fig. 10). The fleshy petal scale, a characteristic feature of the genus and other closely related Pangieac, provided a collection point for nectar droplets during the night (which then pooled in the keeled petals to a lesser extent during the day; Fig. 11). The flower scent was strong, particularly at night, and could be described as somewhat sickly sweet with overtones of wet dog and body odour. Extrorse dehiscence of the anthers on staminate flowers was observed to deposit a significant number of pollen grains on the fine hairs surrounding the anthers, as well as on the filaments (Fig. 12). Mutated carpellate flowers were occasionally found with deformed anthers borne on some staminodes (Fig. 13).

Figs 3-13. Floral morphology and habit of *Ryparosa kurrangii*. (3) flowering takes place in a spectacular flush covering the trunk during June-September; (4) globose buds on staminate flower racemes; (5) pyriform buds on carpellate flower racemes; (6) the calyx (staminate flower shown) irregularly ruptures during floral anthesis; (7) carpellate flowers with a superior ovary; (8) short fleshy staminodes (indicated by an arrow) on carpellate flowers; (9) staminate flowers with united filaments; (10) open flowers (staminate flower shown) are heavy with nectar droplets at night; (11) the fleshy petal scale provides a common collection point for nectar droplets; (12) pollen grains (indicated by an arrow) frequently lodge in hairs surrounding the anthers and on the filaments in staminate flowers; (13) mutated staminode with anther (indicated by arrow).



Flower visitors

All animal interactions observed involved small invertebrates and no flower visitation by vertebrates such as bats was witnessed. Both staminate and carpellate flowers had no obvious morphological adaptations to visitation by specialised insects; however, their small size and relative fragility may preclude larger animals from settling. Most flower visitation took place at night and invertebrates were generally concentrated on flowers with ample nectar. Consistent flower visitation across flowering seasons was observed for a range of invertebrate species. These included numerous small thrips (Thysanoptera) concentrated on and around the petal scales and ant species (Hymenoptera: Formicidae) feeding on flower nectar, including the weaver or green tree ant *Oecophylla smaragdina* (Fabricius). However, the two most abundant invertebrates on *R. kurrangii* flowers were an undescribed species of *Monolepta* Chevrolat *sensu lato* (Coleoptera: Chrysomelidae: Galerucinae; Figs 14, 15) and the mirid *Coridzolon australiense* Carvalho & Gross (Heteroptera: Miridae: Mirinae: Hyalopeplini; Fig. 16).

Both *Monolepta* sp. and *C. australiense* were observed on staminate and carpellate flowers in all *R. kurrangii* populations monitored across numerous flowering seasons. Individuals spent periods of up to 5 minutes on each flower raceme, coming into contact with both anthers and stigmas (on staminate and carpellate flowers, respectively). These insects appeared to be feeding on nectar and perhaps pollen, doing little visible chewing damage to the actual floral organs during flower visitation. The majority of *C. australiense* observed were nymphs, which is a strong indication that *R. kurrangii* may be a breeding host plant. Surveys of *C. australiense* abundance revealed up to 12 individuals spread over 20 racemes on each tree. In contrast, all observed specimens of *Monolepta* sp. were adults that were often seen flying between staminate and carpellate racemes on nearby trees when disturbed. The density of *Monolepta* sp. was also far greater than any other flower-visiting invertebrate on *R. kurrangii*, with conservative estimates of over 300 individuals per tree on some nights.

Discussion

As a genus, *Ryparosa* is little studied and poorly known from field-based interactions. It has rarely appeared in the wider scientific literature since it was first described nearly 200 years ago. Current taxon delimitation within the genus is largely based on vegetative qualities derived from herbarium specimens and many *Ryparosa* species are still imperfectly described in terms of staminate or carpellate flower form (e.g. Ridley 1936, Sleumer 1954, Jarvie and Stevens 1998). An overall unfamiliarity with the genus, particularly in the field, might have led to the situation where the taxon is widely documented as being dioecious (e.g. Sleumer 1954, Hutchinson 1967, Renner and Ricklefs 1995, Jarvie and Stevens 1998).



Figs 14-16. Common invertebrate flower visitors of *Ryparosa kurrangii*. (14-15) adult of an undescribed species of *Monolepta*; (16) nymphs of *Coridzolon australiense*.

By observing tagged populations of *R. kurrangii* in Australian rainforests, it was possible to follow the reproductive biology of individual trees over a number of seasons. This revealed that *R. kurrangii* appears to be consistently monoecious. A distinct confusion over the reproductive details of the Flacourtiaceae *sensu lato* in general was described by van Slooten (1925), who cited examples of *Pangium edule* Reinw. 'bearing male flowers and later on a few fruits' while trying to describe the species as being dioecious. Similar observations were made by Woodson and Schery (1968) in other flacourtiaceous genera. Given that staminate and carpellate flowering periods in *R. kurrangii* were temporally distinct, it would be easy to miss this trait in a once-off sampling of field material. However, *Ryparosa* species have been cultivated in the Bogor Botanic Gardens in Indonesia for well over a century, without any conflicting reports of monoecy (Koorders and Valetton 1900). Reports of both monoecy and dioecy in *Hydnocarpus* and other closely related genera warrant further investigation (e.g. van Slooten 1925).

For *R. kurrangii*, nocturnal nectar production and a strong scent, combined with mass flowering, small open flowers with hairs to trap pollen and a lack of overall colour, fits closely with a beetle pollination (cantharophily) syndrome (e.g. Faegi and van der Pijl 1976, Irvine and Armstrong 1988, 1990, Williams and Adam 1994). While the fragile structure of the flower racemes and the very small size of the flowers would most likely preclude vertebrates (such as bats) as potential pollinators, they should not be ruled out altogether (e.g. Hopper 1980, Crome and Irvine 1986).

Flowers under observation were visited by a range of invertebrates dominated by *Monolepta* sp., *C. australiense* and thrips (Thysanoptera). Thrips have been shown to be effective pollinators for other plant species (Williams *et al.* 2001, Moog *et al.* 2002). However, the lack of wind in the rainforest understorey combined with a weak flying ability means that their role as an efficient pollination vector for *R. kurrangii* is doubtful. The problem of dubious inter-plant visitation also applies to the nymphs of *C. australiense*, which are highly unlikely to be a dispersive life stage of the species. It is generally thought that males of the Miridae are the dispersive phase; however, no observations were made on the movements of adults. Mirids have been implicated as potential pollinators, primarily because of their known pollen feeding strategy and common association with flowers. The fact that many mirid species are host plant specific increases their capacity as pollinators, but most studies to date indicate that they are inefficient (Bohart and Nye 1960) or chance (Wheeler 2001) pollinators. Given that there are increasing linkages between mirids and flower pollination in other tree species (Ashton *et al.* 1988, Corlett 2004), their role as a pollination vector warrants further investigation.

Perhaps the most effective pollination vector in a seemingly generalist approach for *R. kurrangii* may be *Monolepta* sp. Beetles have increasingly been considered as potential pollinators (Young 1986, Irvine and Armstrong 1990), with documentation of specialised interactions. Williams and Adam (1998, 2001) have shown that smooth-bodied invertebrates are inadvertently capable of transporting pollen. The Galerucinae are known to be polyphagous, feeding on pollen and nectar as well as flowers and leaves (e.g. Murray 1982) and observed interactions with *R. kurrangii* would allow for pollen transfer between staminate and carpellate flowers. ANIC specimen records indicate a known distribution range for this *Monolepta* sp. from Palmerston to Cape Tribulation in northern Queensland (C.A.M. Reid, pers. comm.). Therefore, with a distribution much wider than that of *R. kurrangii*, it is unlikely that the observed *Monolepta* taxon is host specific. Studies on other trees, such as *Alphitonia excelsa* (Fenzl) Reiss. ex Benth. (Rhamnaceae) and *Syzygium cormiflorum* (F. Muell.) B. Hyland (Myrtaceae), also list a number of *Monolepta* taxa as flower visitors (Crome and Irvine 1986, Williams and Adam 2001).

This study has addressed two areas where a lack of knowledge and a reliance on herbarium specimens over field observations in plant systematics are clearly impeding our understanding of plant reproductive biology and plant-pollinator interactions. Firstly, temporally separated monoecious flowering may be more widespread in *Ryparosa* and other closely related taxa than is currently thought. Further field studies of tagged trees will be required to confirm if this trait is ubiquitous in *R. kurrangii* and, perhaps, characteristic of a wider range of closely related genera. Secondly, the documentation of what might be an invertebrate pollination system adds to the limited number of pollination studies from Australian tropical rainforests. Importantly, more work now needs to be done in extending our knowledge of the pollination efficiency and dispersal distance of *R. kurrangii* flower visitors, given their potential impact on gene flow within and between populations of this rare tree.

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